COELOMIC PRESSURES IN SIPUNCULUS NUDUS

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Most invertebrate animals are characterized by lack of constancy of their internal pressure. In sipunculids, for example, the pressure may fluctuate within a short time between nearly zero and the equivalent of the blood-pressure of man. Pressure variations of this magnitude never occur within closed vascular systems. They are possible only in continuous spaces filled with fluid and enclosed by a muscular body wall. In such systems the main function of pressure is not circulation, but hydraulic work. In "closed" systems with more constant fluid pressure, hydraulic work is accessory. This latter function has been recently investigated in the annelid *Arenicola* by Chapman and Newell (1947). In the present study, pressure variations in *Phascolosoma* and *Sipunculus* will be analyzed mainly in relation to body movements. Coelomic pressure has long been recognized as essential in the digging activities of sipunculids; Uexküll (1903) measured in *Sipunculus nudus* pressures up to a maximum of 6 cm. Hg, i.e. 80.4 cm. of water, during burrowing in sand. Information on sipunculids is offered in the monograph of Baltzer (1934).

The hydraulic function of pressure in body fluids is wide-spread throughout the animal kingdom as shown in the following examples of water vascular systems. In holothurians pressure in the water vascular system is essential for tentacle erection (Zuckerkandl, 1948). In those sipunculids which possess tentacles, there is a water vascular system controlling their turgescence. In acanthocephalans, the water-vascular system is reported to be related to the erection of the proboscis (Hamann, 1891; Rauther, 1930).

In the polychaete *Arenicola,* burrowing depends on hydraulic pressure in the body cavity (Chapman and Newell, 1947). Pentastomids seem to be able to set up relatively high body fluid pressures, used for the extension of their parapodia and other appendages (Heymons, 1926). In priapulids, the evagination of both the proboscis and the caudal appendage is due to body fluid sent under pressure into the parts to be evaginated (Fischer, 1925). Bryozoa possess a hydraulic pump mechanism which serves the evagination of their tentacles (Delage and Herouard, 1897). In nemerteans the protrusion and reversion of the proboscis is brought about by coelomic fluid pressure, set up by the contraction of the muscular proboscis, while retraction of the proboscis is largely due to contraction of the retractor muscles (Böhmig, 1929). A similar mechanism of proboscis eversion and retraction exists in sipunculids (Baltzer, 1934).

In the foregoing examples, body cavity fluid or water vascular fluid is responsible for hydraulic action. Examples of hydraulic action of vascular blood are also reported. Polychaete and oligochaete annelids which dig channels in earth or sand (*Arenicolida, Glassoscolecida, Megaloscolecida, Lumbricida*) possess a strongly developed vessel running laterally along the oesophagus (vas extraoesophagale)

(Fuchs, 1906). Brücke (1925, p. 852) believes that turgescence of this vessel might favor digging. The leech *Herpobdella* has a capillary net on both its anterior and posterior suckers. When suction occurs, blood from the neighboring vessels streams into the capillaries, thus taking part in the mechanical effect (Emden, 1929). Also in *Herpobdella* the spermatophores are squeezed out during the sexual act by an increase of blood pressure in a specialized organ. In sexual function the hydrostatic pressure of blood is often used mechanically: e.g. for penis erection in mammals. In pelecypod molluscs the swelling of the foot is due to hydraulic action of the blood (Buddenbrock, 1939). The stretching of the ocular tentacle of the common snail is based simply on relaxation of the retractor muscle. The existing blood pressure is sufficient to extend the tentacle (Buddenbrock, 1939).

These examples suffice to show the widespread use made of body fluids for hydraulic work.

Materials and Methods

Phascolosoma gouldi was furnished through the kindness of the supply department at the Marine Biological Laboratory in Woods Hole, Mass. *Sipunculus nudus,* on which most of the work was done, was collected on the beach of Morgat, Brittany.

The *Phascolosoma* used were 6 to 10 cm. long, the *Sipunculus* sometimes reached a length of 18 cm. in the expanded state.

Pressure was recorded by inserting straight capillary glass tubes into the coelom of the sipunculid as used by Inada (1947) in crayfish and mussels. Capillaries with a bore of 1 to 1.5 mm. were selected and their zero point determined. The pressures are expressed in cm. of coelomic fluid. Temporary withdrawal of fluid from the body cavity into the capillary did not affect the animals. To obtain a coordinated record of pressures and body movements a method of registration on a kymograph was used. The moving meniscus in the capillary tube was closely followed by means of a horizontal metal thread which was connected through a lever system with a writing point, applied against the drum of the kymograph. While one person recorded pressures, another person inscribed on the kymograph record, by a system of conventions, the movements observed on the animal.

Discussion

Types of movement. In *Sipunculus,* three types of movement may be distinguished: swimming, defense movements, and burrowing.

Swimming is observed frequently in freshly collected specimens kept in sea water without sand. In the regular, beat-like bendings of the body all circular muscles are contracted, while the longitudinal muscles of the dorsal and ventral sides contract and relax alternately (Uexküll, 1903). Swimming movements are accompanied by alternate rises and falls in pressure.

When strongly excited, *Sipunculus* and *Phascolosoma* execute defense movements. The two extremities of the body may be brought together and often cross, while the body of the animal turns around its longitudinal axis. The pressure, during this action, is considerably higher than during swimming movements. In

Phascolosoma it reaches commonly 50 cm., in *Sipunculus* commonly 70 to 80 cm. of body fluid.

Usually the defense reaction does not consist in active movements, but in a state of immobility accompanied by high turgor and the reduction of the body surface. The longitudinal muscles contract to their maximum. In both *Sipunculus* and *Phascolosoma* pressures reach top values around 100 cm. of body fluid. There seems to be no relation between maximum pressure and body size. The highest pressure observed—108 cm.—was in a small specimen of *Phascolosoma.*

Burrowing type movements and corresponding pressures. On animals put in a glass jar filled with sea-water and devoid of sand, five to six phases may be distinguished in the cycle of burrowing type movements (*Sipunculus*):

1) At the start there is formation of a "hump," i.e., a bending upwards of the central part of the body in a nearly vertical plane. At the same time the pressure begins to rise from initial values of 2–3 cm. of water.

2) While the hump is maintained, the eversion of the proboscis begins speedily. The pressure continues to rise.

3) The proboscis is partly protracted (usually about two-thirds) while the hump is being released. From that instant on the progression of the proboscis is slower. Simultaneously the pressure, reaching a maximum, mostly between 10 and 30 cm., stops rising, and starts falling immediately. The fall is usually completed before the next phase begins.

4) The tentacles appear. They are set free by a slight recession of the anterior extremity of the proboscis. Pressure remains constant, or, sometimes, drops very little.

5) Tentacles and proboscis are being retracted. During this action, a further, very slight fall of pressure (2–4 mm.) takes place. This fall may fail to occur or set in only after completion of proboscis retraction. Pressure attains exactly or nearly the level at which it started at the beginning of the burrowing cycle.

6) A period of immobility, of constancy of pressure. This phase is usually skipped when the animal is in a state of activity. In that case, phase 1 succeeds phase 5.

When *Sipunculus* remains in its feeding posture, the cycle is interrupted after phase 4.

During fast burrowing, which is accompanied by no tentacular eversion, the pressure, in preparation for the next protraction, rises while the proboscis is being retracted. In that case, high pressure is already present when the retractor muscles suddenly relax. The proboscis is, as it were, shooting out against the sand in full force. Such cases are illustrated by Figures 1 and 2, drawn after kymograph records.

The formation of the hump is synchronized with rise in pressure and the disappearance of the hump with fall in pressure. On the other hand, rise and fall in pressure are not essentially related to the protraction and retraction of the proboscis, as might have been expected *a priori.* Indeed, hump and definite pressure rise may fail to occur, while the proboscis is protracted normally, although more slowly than under marked pressure (Fig. 3). In several instances, the pressure was seen to remain constant at 1 cm. of body fluid during the whole protraction-retraction

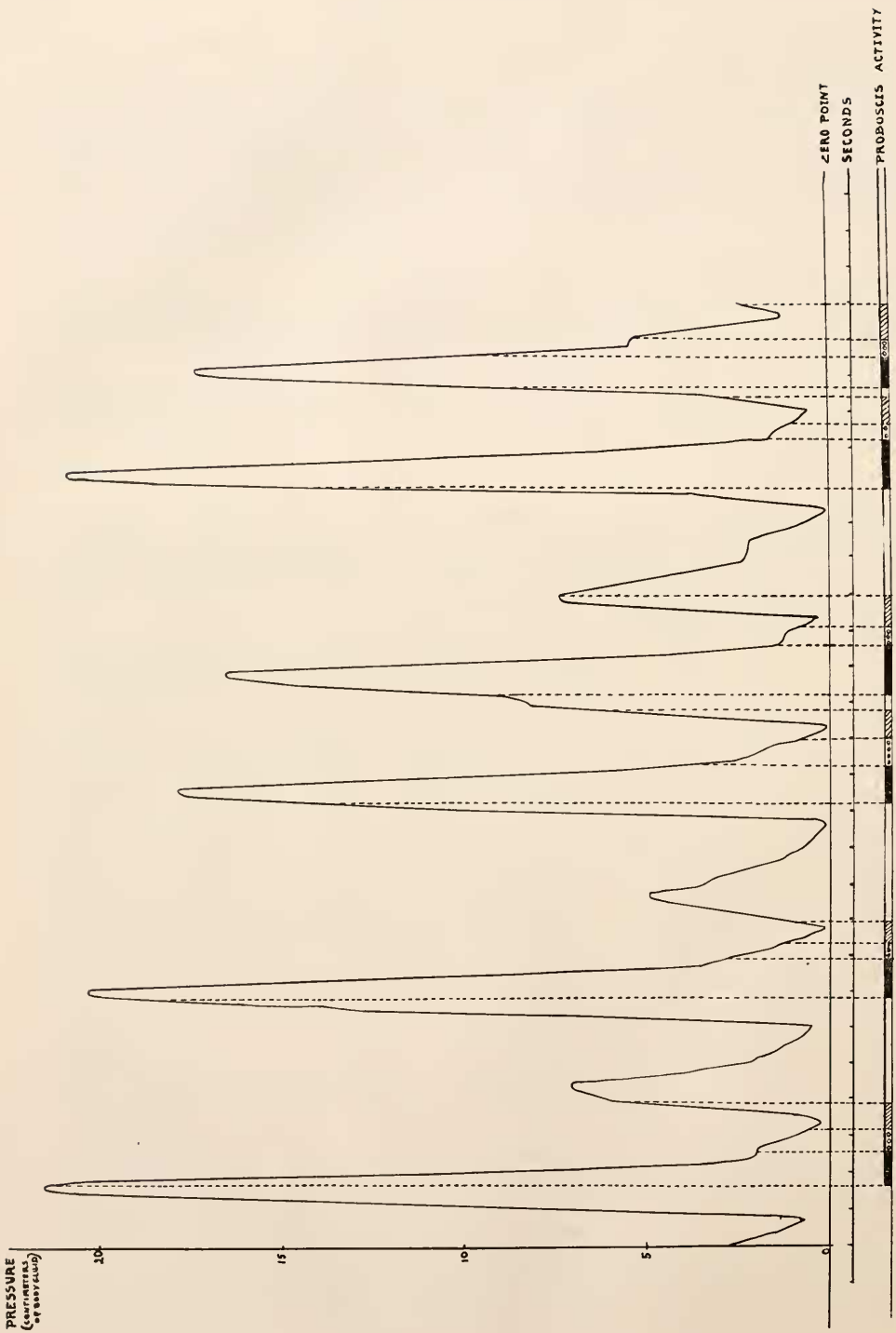

FIGURE 1. Data from kymographic record of coelomic fluid pressures in cm. coelomic fluid, and corresponding movements of proboscis of *Sipunculus nudus*. Time line: six second intervals. Proboscis activity indicated by following conventions: ■ proboscis being extended, ▨ proboscis extended, ▧ proboscis being retracted, □ proboscis retracted.

operation. However, protraction never occurred when the pressure was below 0.9 cm. of body fluid. The cessation of pressure rise and onset of fall may correspond to various states of protraction of the proboscis. Exceptionally the pressure rise may continue throughout the process of proboscis retraction. These irregularities illustrate the lack of strict coordination between pressure variations and proboscis protraction. Evidence of disjunction between the cycle of movements and the cycle of pressures is recorded by the kymograph record in Figure 1. There

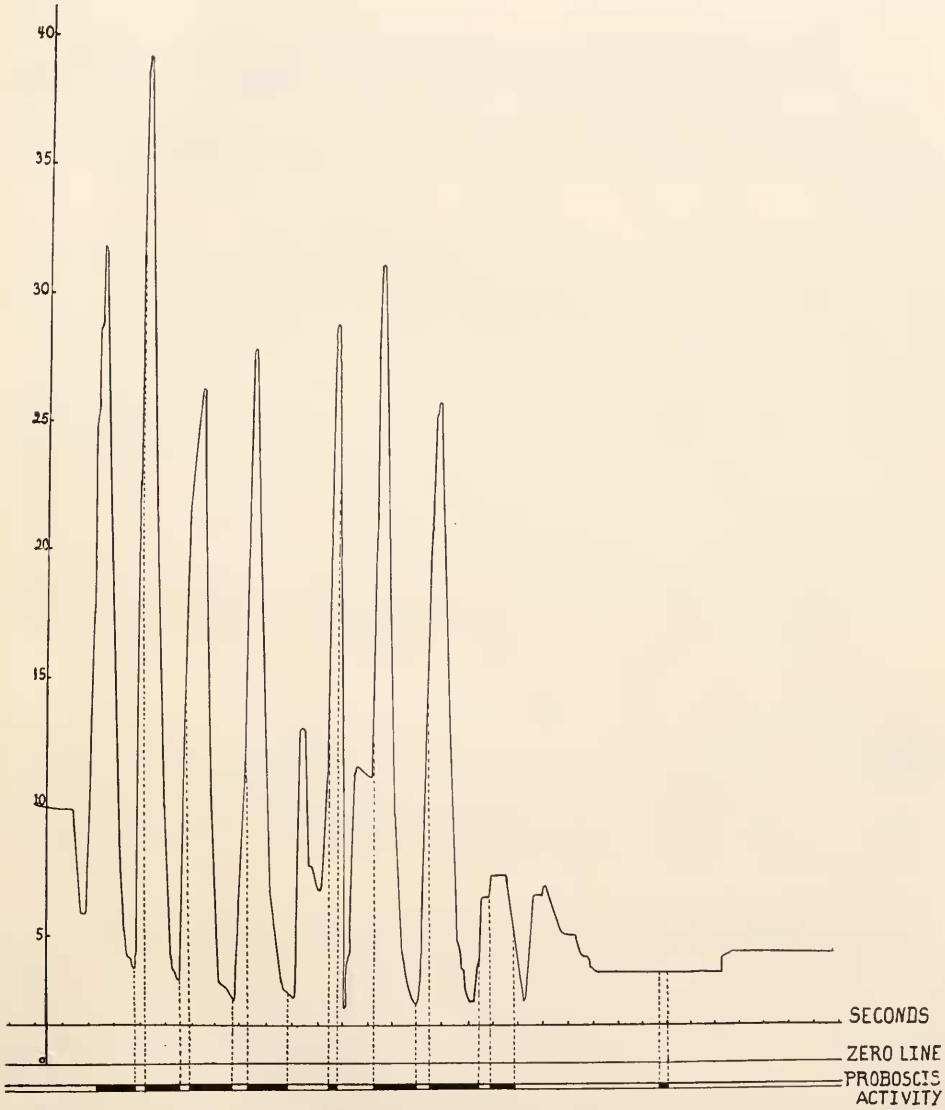

FIGURE 2. Pressure (ordinate) in mm. coelomic fluid in *Sipunculus nudus* recorded on kymograph. ▬ proboscis extending, ▭ all other phases of proboscis movements.

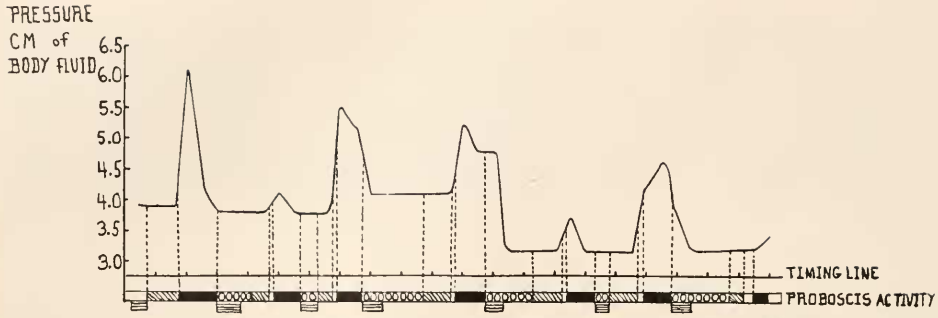

FIGURE 3. Pressure (ordinate) in coelomic fluid and activity in *Sipunculus nudus* recorded with aid of metronome beat every third second. Timing line gives 10 second intervals. Conventions for record of proboscis activity as in figure 1 with addition ▤ tentacles being extended.

we see, in several instances, one cycle of movements coinciding with two pressure cycles. The pressure cycle keeps firmly to its established timing, while the timing of the movement cycle is less constant; though keeping pace sometimes with the pressure cycle, at other times it is twice as slow. It should be noted that during what might be called an "extra-systole"—a pressure cycle not coordinated with proboscis protraction—the pressure never rises as high as it does otherwise. Even in this case a certain relation between movement and pressure is, then, maintained; very high pressures seem to be set up only when proboscis protraction really occurs.

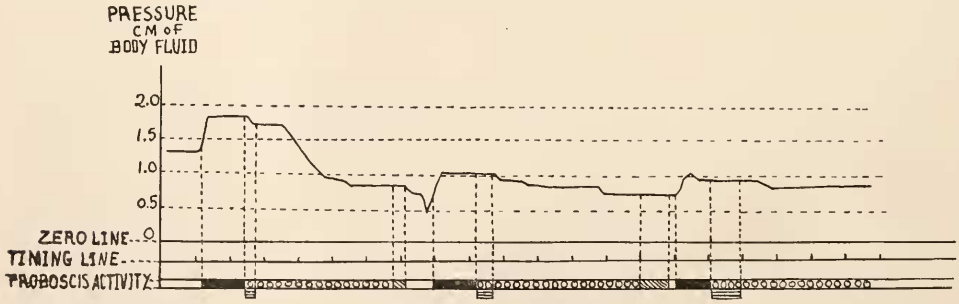

FIGURE 4. *Sipunculus nudus*, pressure and activity noted every fourth second with aid of metronome. Six second intervals on time line. Conventions for activity as in figure 3.

The 5th and 6th pressure rises in Figure 2 are illustrations of this. Here pressure has no time to drop to the usual minimum, before the rise accompanying protraction occurs and the movement cycle is not exactly half as slow as the pressure cycle. Thus the rhythmicity of the pressure cycle is upset to some extent. Depending on how soon after the "extra-systole" the large rise accompanied by proboscis protraction sets in, the "extra-systole" may be represented by a whole spike, as in Figure 1, or be reduced to a simple discontinuity of what appears to be one single pressure rise spike (6th spike on Figure 2).

The pressure rise may set in before the formation of the hump. In this case the appearance of the latter is characterized by a marked increase in speed of the rise.

The basic tonus, represented by the pressure minimum attained with phase 5, may remain constant during several consecutive burrowing cycles and then rise to a different level (Fig. 4).

The amplitude of pressure changes during burrowing movements in free water is very variable. In *Sipunculus* pressure during proboscis protraction was seen to attain maxima ranging from 1 cm. (Fig. 3) to about 40 cm. (e.g. animal I of table below). Maximum pressures registered during proboscis eversion in different specimens of *Phascolosoma* follow: 11.4; 12.4; 15.0; 16.0; 17.3; 21.3; 25.0; average: 16.9 cm.

The following table gives the relation between average pressure extremes and intervals between onsets of pressure rise in eight specimens of *Sipunculus*.

Animal	Average time elapsing between onset of two pressure rises (seconds)	Number of cycles averaged	Highest pressure reached (cm. of body fluid)	Average pressure minimum (cm. of body fluid)
I (Fig. 2)	12.7	8	39.6	2.6
II (Fig. 1)	15.6	11	21.2	0.4
III	17.3	6	20.1	2.5
IV (Fig. 4)	18	6	6.1	3.6
V	18	3	8.7	2.3
VI	18.4	6	25–30	—
VII	18.5	5	23.4	0.9
VIII	20.5	7	24.2	2.5

From these eight experiments, the average time elapsing between two pressure rises is about 17 seconds. The shortest time intervals are obtained in animal I which also showed the highest pressures, but in those with low maximum pressures the time intervals remain near the average (IV, V). The rhythmicity of pressures therefore seems largely independent of their magnitude. During most experiments the minimum pressures were nearly constant.

Proboscis eversion in *Sipunculus* occurs whatever the position of the animal, and not only, as Baltzer (1934) claims, when it lies on its ventral surface.

Pressures and movements during burrowing in sand. Specimens of *Sipunculus* were placed in a glass aquarium filled with sand, between a glass plate and the aquarium front. Since little space was available for lateral movements, the worm was often forced to slip along the aquarium front and its movements could thus be watched.

At the start of burrowing, pressures were similar to those given in the preceding section. As the animal gradually penetrated into the sand, the maximum pressures increased very considerably, the minimum pressures slightly. The increase in maximum pressures was sometimes strikingly gradual (Fig. 5). As long as only part of the animal's body was under sand, the maxima did not exceed those commonly observed during digging type movements in free water. Once the animal was about two inches below the surface, maximum pressures around 90 cm. were commonly reached (top value on record: 96 cm.). During these highest pressures greatest speed of progression was obtained. When the animal returned to low speed progression, the pressure maxima decreased markedly. Under com-

paratively low pressures the progression was never fast. High speed progression is not possible before the animal is wholly under sand. Indeed, the "hump" is effective under these conditions only as explained below. Since fast progression requires high pressure and is possible only when the animal is nearly completely under sand, pressure gradually increases as it becomes effective.

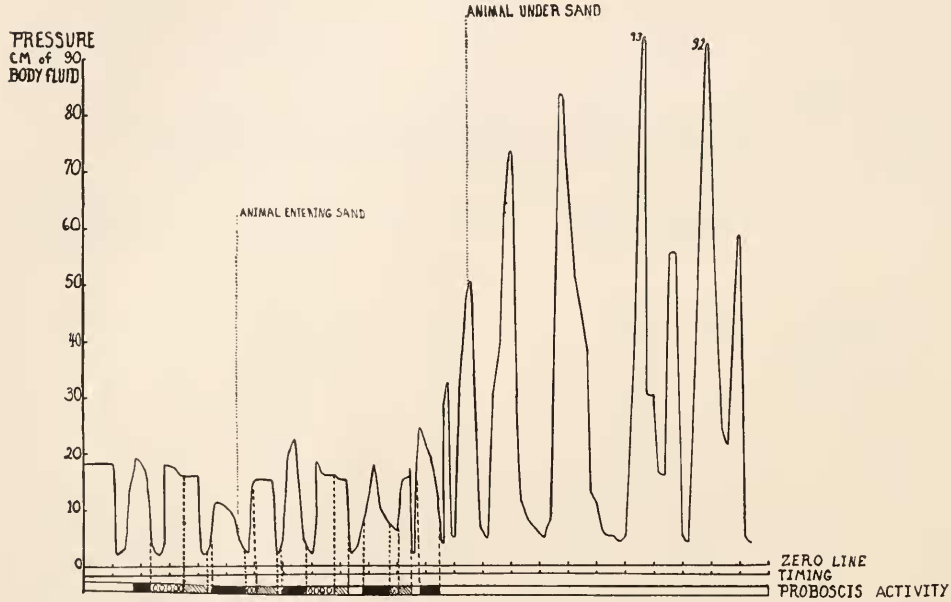

FIGURE 5. *Sipunculus nudus*, coelomic pressure and activity recorded every third second with aid of metronome. Conventions for proboscis activity as in figures 1 and 3. Time line, 10 second intervals.

Figure 6 shows how pressure variations and body movements are coordinated during burrowing under sand. The results are similar to those for burrowing movements in water except that the maxima often reach very much higher values. The period of low maxima corresponds to one of lower burrowing activity; the animal progresses less speedily and remains longer in the "feeding position" (proboscis and tentacles stretched out).

Under sand, proboscis protraction has been seen to continue under a pressure as low as 3.2 cm.

As in animals kept in free water, tentacle eversion was brought about by a retraction of the distal section of the proboscis. In this way the tentacles are set free within a cavity prepared beforehand by the burrowing proboscis and are protected from rough contacts with the sand.

Figure 5 affords evidence that the normal correspondence between burrowing cycles and pressure cycles may be systematically upset during burrowing in sand, just as it was occasionally during movements in free water. One burrowing cycle consistently corresponds to two pressure cycles. (The movements could not be followed during the later part of the record.) Proboscis retraction does not occur

around the time of a pressure minimum, as in the case shown by Figure 1, but coincides with the top of a pressure spike. Curiously, retraction occurring at the moment of a pressure maximum seems to prevent the pressure from falling. A pressure plateau is maintained near the maximum as long as retraction lasts. The pressure spikes are always influenced by changes in the proboscis cycle, yet the rate at which the spikes follow each other may not be. Thus the two cycles (pressure and proboscis movements) may occupy various positions in time with respect to each other.

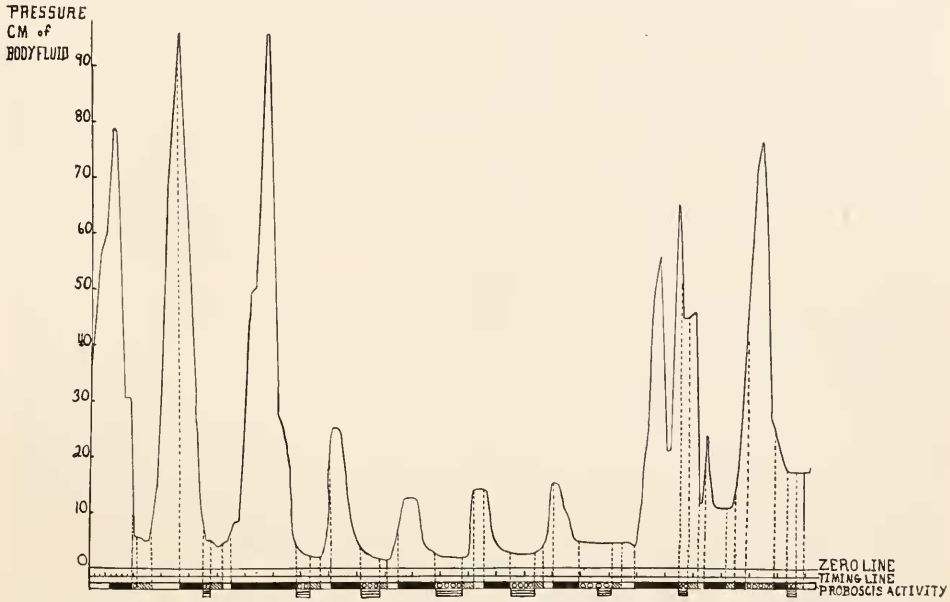

FIGURE 6. *Sipunculus nudus.* Coelomic pressures and proboscis movements recorded with aid of metronome every third second. Conventions as in figure 3. Time intervals, 10 seconds.

In conclusion, the motor nerve centers controlling contraction of the body wall appear to some degree independent of those for the movements of the proboscis, i.e., contraction and relaxation of the retractor muscles.[1] Moreover, pressure is likely to have a function partly independent of proboscis protraction.

The function of pressure during burrowing. With respect to its function, one may consider pressure from three points of view:

1) pressure necessary for proboscis eversion in absence of any resistance.
2) pressure necessary for the proboscis to overcome the resistance of the milieu.
3) pressure necessary to insure the progression of the animal in its milieu.

1. When the proboscis does not meet with any resistance, it can be protracted, as stated above, under exceedingly low pressure (minimum 0.9 cm.). Low pressure eversion differs from eversion under high pressure by being slow and very regular. A given low pressure is sometimes maintained although, with proboscis eversion, the

[1] The muscles of the proboscis wall are not important in protraction. See below.

volume of the body cavity gradually increases. Thus is brought out the ability of the relaxed *Sipunculus* muscle to compensate exactly for any variation in pressure by corresponding variations of its length, so as to maintain a constant state of tension.

In the absence of coelomic pressure, proboscis protraction was never observed. An active animal was cut open along the dorsal midline, so as not to injure its nerve cord. Thus deprived of the possibility of setting up pressures, it was put back into sea-water. Although the muscles of the animal remained able to display activity, no eversion of the proboscis occurred. Therefore the presence of a head of pressure of at least 0.9 cm. of body fluid seems to be the necessary condition for proboscis eversion.

The question was raised whether this condition is also a sufficient one. In other words, do the muscles of the proboscis play any active part in eversion? The body of a specimen of *Sipunculus* was cut through transversely at the level of the anus and the posterior part of the worm discarded. The anterior part was kept immersed for several minutes in a solution of iodo-acetic acid (M/50), supposed to interfere with muscular contraction. Then the proboscis was drawn back by pulling on the retractor muscles. The fragment of the animal was slipped over the tip of a wooden rod and kept under sea-water. The system was made nearly water-tight by tying a thread over the cut end of the worm stretched over the stick. A capillary tube was introduced behind the base of the proboscis for measuring pressure, and sea-water was injected into the body cavity with a syringe. At 1.1 cm. of coelomic pressure (measured in cm. of sea-water), the proboscis was seen to unroll very slowly, part way. As the pressure rose to 1.7 cm., the proboscis extended quickly and thoroughly. The tentacles came out at the end of its eversion. Since the muscles of the proboscis poisoned with iodo-acetic acid did not display any activity, it is probable that active participation of the proboscis muscles is not needed for proboscis eversion and that very low pressure is indeed sufficient to bring about this eversion.

What, then, is the role of the proboscis muscle? It seems to be at least two-fold. One function is the retention of the proboscis inside the body-cavity. The muscles of the proboscis seem indeed able to help the retractor muscles, if not to replace them in that role. In animals whose retractor muscles had all been cut, the proboscis still resisted pressure and did not unroll. A second role of the proboscis muscles must be related to the "thixotropic" effect of digging, which will be discussed below.

2. We shall deal now with the pressure necessary to overcome the resistance of the sand.

The experiment reported above (setting up measured pressure in the body cavity of an anterior portion of a *Sipunculus,* the proboscis muscle being kept from contracting) was repeated on the same fragment of *Sipunculus* under 2 cm. of sand. Pressure was raised up to 9 cm. of sea-water, while the proboscis protruded only very slightly and was unable to continue its eversion.

On the other hand, in a normal animal burrowing in sand, proboscis eversion was observed, in one instance, as reported above, under a pressure of only 3.2 cm. of body fluid, and in a number of instances under slightly higher pressures.

These two results seemed inconsistent. And *a priori* it would not have seemed reasonable to assume that pressures as low as 3.2 cm. could overcome the resistance of the sand. It was impossible to drive out by pressure, under sand, the inverted

finger of a rubber glove filled with water. The finger of a rubber glove surely meets a much higher resistance than the slender proboscis of *Sipunculus*. Nevertheless eversion of the proboscis in sand under a pressure of 3.2 cm. seemed hardly understandable.

The work of Chapman and Newell (1947) appears to offer the clue to this question. These authors, studying pressures in *Arenicola*, showed that very low pressures are sufficient for penetration in muddy sand. This kind of sand, which also is the medium of *Sipunculus*, behaves as a thixotropic colloidal system. "If the sand is prodded several times with a stick its resistance diminishes, and it remains in a semi-fluid state as long as the prodding continues." With an anesthetized proboscis or the water-filled finger of a rubber glove this thixotropic effect cannot be obtained, hence the failure, in these cases, to obtain protraction in sand under low pressure. However, the extending proboscis of *Sipunculus* probably has an effect similar to the prodding of a stick, and in this respect the muscles of the proboscis must play an outstanding rôle.

3. The function of high pressure, unnecessary to proboscis eversion even under sand, seems to be to insure efficient progression of the worm in the sand. Large pressure rises have been reported always to be accompanied by a bending of the central part of the body. This bending also occurs under sand, as far as compatible with the resistance of the walls of the burrow. The central part of the worm is thus immobilized on a given spot by the pressure exerted against these walls. The body is therefore prevented from being pushed back during the action of proboscis protraction. At the same time, the high pressure insures a speedy progression of the proboscis, thus increasing the "prodding" effect. High pressure seems therefore to have a triple role: to maintain the hump, which serves as anchorage in the burrow; to favor the thixotropic action of the proboscis; and to insure speedy progression.

One may wonder how the animal can do without the hump during the last slow phase of proboscis eversion. It should be remembered that the hump is not in all circumstances a necessary condition for proboscis progression. Indeed, when the proboscis first penetrates into the sand, the rest of the body, including the hump, is still outside it. Nevertheless the animal is able to progress slowly.

Yet during the more energetic phase of burrowing, the hump, no doubt, affords a necessary fulcrum. It corresponds to the "collar," a swelling appearing on the distal extremity of the proboscis. It is assumed that, due to a grip on the sand at this swelling, the body can be drawn forward.

The hump has another important function. It creates on one side a hollow space between the wall of the burrow and the animal's body. In this space a backward flow of sand particles was consistently observed. Apparently the sand stirred up by the proboscis during the first phase of its protraction is thus flowing back, leaving ahead the space necessary for the progression of the body. The body has indeed a much larger diameter than the proboscis and could not follow the proboscis, if the latter burrowed a channel of just its size. The effects on the sand of the thixotropic stirring action of the proboscis were thus directly observed, and in relation to them the hump appears to be indispensable. Considering the resistance of the walls of the burrow, this hump can develop in sand under high pressure only.

The necessity of high pressure for progression in sand was shown by Uexküll (1903). He destroyed in a specimen of *Sipunculus* the posterior part of the nerve cord. The posterior part of the body was distended, high pressure could not be developed and the animal was not able to progress in the sand. If Uexküll then cut off the paralyzed posterior section and closed the opening with a rubber stopper, the anterior half of the worm was seen to disappear in the sand within a few minutes.

The role of pressure in circulation of coelomic fluid. Circulation of coelomic fluid in *Sipunculus* is brought about by several factors: the ciliation of the coelomic epithelium (Mayer, 1929), the stirring action of the urns—little ciliated organelles swimming around freely in the body cavity—and the movements of the body wall. The effect of cilia is probably the only one acting consistently in the sense of fluid movement in a closed circle throughout the body.

It is clear that a mechanical action on body fluids cannot be qualified as being "circulatory" in nature, unless it shows some rhythmicity and constancy during at least a certain length of time. The question was raised whether digging, constituting one of the few rhythmical activities of the sipunculid, may have a sufficiently regular influence to cause circulation of coelomic fluid.

In order to study the effects of pressure variation during burrowing movements from this point of view, a few small air-bubbles were injected into three specimens of *Sipunculus*. The animals were placed on a glass plate over a light so that the bubbles were visible. Care was taken to keep the animals in horizontal position. A regular movement of air bubbles during proboscis movements was observed in the anterior region of the body only. At the start of proboscis eversion the bubbles were shifting anteriorly, at the start of retraction caudally. Few shifts were observed in the middle and posterior regions. It is concluded that during burrowing movements, significant pressure gradients are rhythmically established in the front region only. They have an effect on the movements of coelomic fluid.

Some simultaneous measurements of pressure in the anterior and posterior part of the body were compatible with the air bubble experiment, the pressures in the posterior capillary rising and falling faster than those recorded by the anterior capillary.

Summary

The relationship between coelomic pressures and body movements has been investigated in *Phascolosoma gouldi* and, mainly, *Sipunculus nudus*.

During "defense movements," pressure in *Phascolosoma* is commonly 50 cm. of water, in *Sipunculus* 70 to 80 cm. During "defense immobility," the highest pressure recorded, in *Phascolosoma,* was 108 cm. There does not seem to be a relation between body size and maximum pressure.

Six phases of burrowing movements have been distinguished in *Sipunculus* and related to coelomic pressure. An important pressure rise coincides with a bending movement of the central part of the body. This "hump" and the high pressures associated with it have functions which are described. Very low coelomic fluid pressures suffice to cause eversion of the proboscis. Pressure is a necessary and sufficient condition for proboscis eversion in free water, while in sand the proboscis muscles seem to play an essential role during proboscis eversion in relation to the thixotropic property of stirred sand.

During most experiments, minimum pressures were very constant, while maximum pressures varied a great deal. During burrowing movements in free water, the highest pressure recorded in *Phascolosoma* was 25.0 cm., in *Sipunculus* 39.6 cm. of body fluid. During burrowing in sand, pressure of 96 cm. water was reached by *Sipunculus*.

The frequency of pressure cycles seems to be independent of the absolute pressure.

The coordination between the cycles of pressure and proboscis movements is variable. Therefore the retractor muscles and the muscles of the body wall are probably dependent on nervous centers which are not closely associated.

Pressure variations during burrowing have an influence on circulation of coelomic fluid.

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